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Neotoma alleni.

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Neotoma alleni Merriam, 1892
Allen's Woodrat

Neotema alleni Merriam, 1892:168. Type locality Manzanillo, Colima.

Hodomys vetulus Merriam, 1894:236. Type locality Tehuacán, Puebla.

CONTEXT AND CONTENT. Order Rodentia, Family Cricetidae, Subfamily Cricetinae. The genus *Neotoma* contains four Recent subgenera and approximately 20 Recent species. *Neotoma alleni* is the sole member of the subgenus *Hodomys*. Four subspecies of *Neotoma alleni* currently are recognized (see Kelson, 1952; Hall and Kelson, 1959:705–706):

N. a. alleni Merriam, 1892, see above.

N. a. elattura (Osgood, 1938:475). Type locality Chilpancingo, Guerrero, according to Osgood but given as Cuapongo, Guerrero (in vicinity of Chilpancingo), by Kelson (1952: 242).

N. a. guerrerensis (Goldman, 1938:498). Type locality Acapulco, Guerrero.

N. a. vetula (Merriam, 1894), see above.

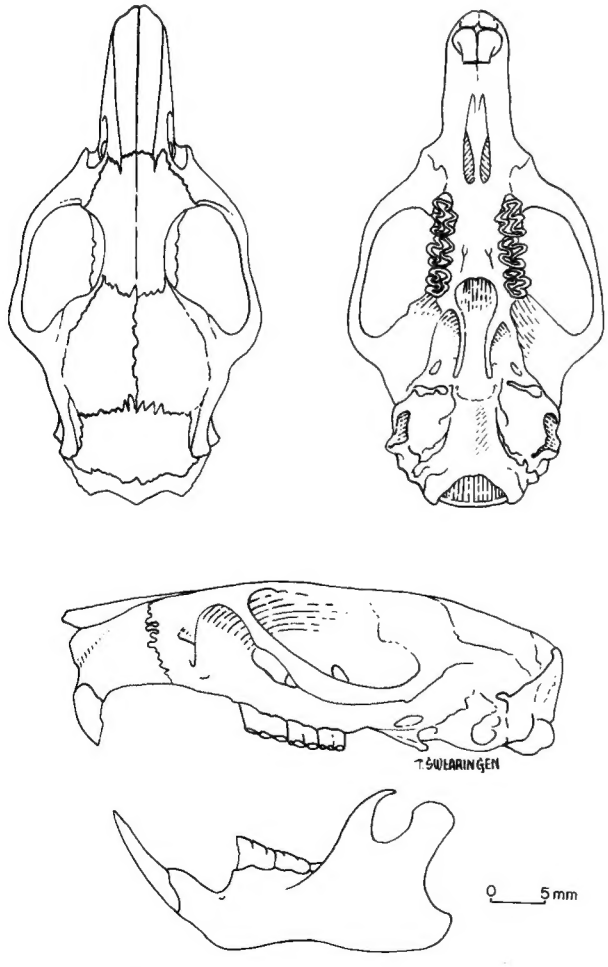

FIGURE 1. Dorsal, ventral, and lateral views of cranium, and lateral view of lower jaw of *Neotoma alleni alleni*, KU 87656, female, from 5 km NNW Barro de Navidad, Jalisco. Illustration by Thomas Swearingen.

DIAGNOSIS. The following diagnosis applies to both subgenus and species: form ratlike; size large for genus; cranium long and narrow (figure 1); supraorbital ridges tending to extend over parietals; incisive foramina long, narrow; bullae small; sphenopalatine vacuities closed; coronoid process of mandible high. Dentition i 1/1, c 0/0, p 0/0, m 3/3; enamel pattern of occlusal surface of last lower molar (m3) S-shaped rather than having two transverse loops as in all other members of the genus (figure 2); first and second upper molars four-rooted, third upper molars three-rooted. Upper parts rich reddish brown to dusky brown; underparts plumbeous washed with white, sometimes faintly buffy; tail sparsely haired, dusky above and below in some populations, becoming whitish below in others. For additional information see Merriam (1894), Ellerman (1941), and Hall and Kelson (1959).

GENERAL CHARACTERS. Mean and extremes of external measurements in millimeters of two males and six females of *Neotoma alleni alleni* (largest subspecies) from Sinaloa (Birney and Jones, 1972:204) are as follows: total length 432.4 (417 to 446); length of tail, 197.9 (189 to 206); length of hind foot, 44.4 (43 to 45); length of ear, 31.0 (28 to 33). Mean and extremes of selected cranial measurements in millimeters of four males and six females from Sinaloa are as follows: greatest length of skull, 53.2 (50.2 to 55.8); zygomatic breadth, 26.4 (23.9 to 28.0); least interorbital constriction, 5.5 (5.2 to 6.2); mastoid breadth, 18.5 (17.5 to 19.1); length of rostrum, 21.6 (20.4 to 22.4); breadth of rostrum, 8.0 (7.5 to 8.7); length of maxillary toothrow, 11.0 (10.7 to 11.7). The average weight of these 10 individuals was 367.6 (291.0 to 451.5) g.

External and cranial measurements in millimeters of an adult female *Neotoma alleni elattura* (possibly the smallest subspecies in size) are as follows (Genoways and Jones, 1973: 17): total length, 368; length of tail, 158; length of hind foot, 37; length of ear, 32; greatest length of skull, 46.3; zygomatic breadth, 24.4; interorbital constriction, 5.6; mastoid breadth, 17.2; length of nasals, 16.6; length of incisive foramen, 10.6; length of palatal bridge, 7.7; length of maxillary toothrow, 9.4.

Measurements for other specimens are given by Merriam (1892; 1894), Elliot (1904), Goldman (1938), Osgood (1938), and Goodwin (1969). Kelson (1952) briefly characterized the four currently recognized subspecies of *Neotoma alleni*.

DISTRIBUTION. *Neotoma alleni* occurs in western and central México from southern Sinaloa to southern Guerrero and northern Oaxaca (figure 3). Localities from which speci-

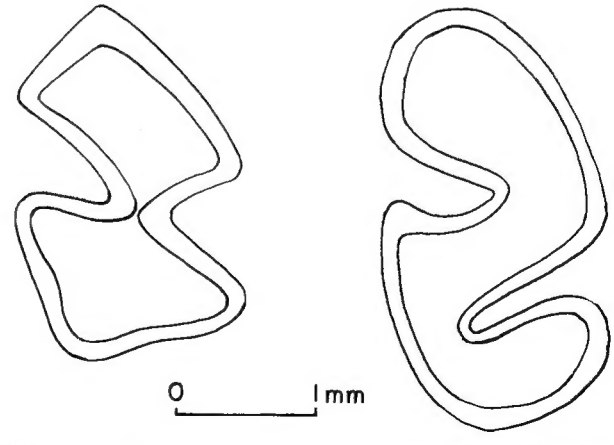

FIGURE 2. Occlusal views of the third lower molars of *Neotoma mexicana* (left, KU 112389) and *Neotoma alleni* (right, KU 87656). Illustration by Thomas Swearingen.

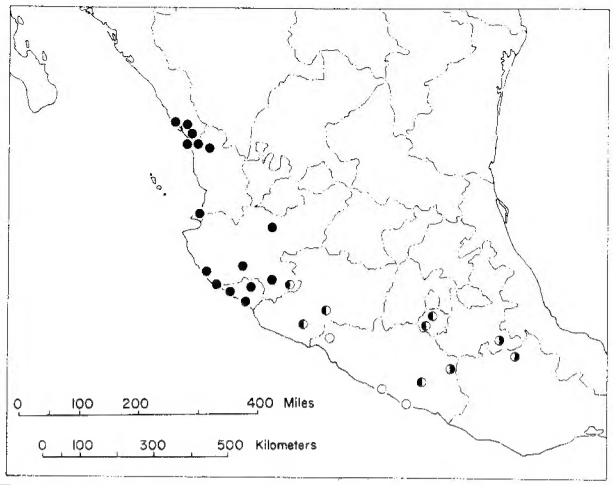

FIGURE 3. Map showing the geographic distribution of *Neotoma alleni* in western and central México. Subspecies are *N. a. alleni* (solid symbols), *N. a. elattura* (half-solid symbols left), *N. a. guerrerensis* (open symbols), and *N. a. vetula* (half-solid symbols right).

mens of each subspecies have been obtained are listed beyond in approximate north to south order within each state; localities omitted from Figure 3 to preclude undue crowding of symbols are italicized.

Neotoma alleni alleni.—SINALOA (Birney and Jones, 1972, unless otherwise noted): Isla Palmito de la Virgen, 15 ft.; Rosario (Goldman, 1938); 27 km. S Escuinapa; *Palmito [about 10 mi. NW Teacapán], 20 ft., Isla Palmito del Verde*; 8 mi. NNW Teacapán, Isla Palmito del Verde; ½ mi. S Concepción [= La Concha], 250 ft. NAYARIT: Acaponeta (Hall and Kelson, 1959); Banderas [= Valle de Banderas] (Elliot, 1907; Hooper, 1960). JALISCO (Genoways and Jones, 1973, unless otherwise noted): 7 mi. N Guadalajara, 4100 ft.; 6 mi. E Limón, 2700 ft.; Chamela Bay (Hall and Kelson, 1959); 10 mi. SE Tuxpan, 4200 ft.; 5 km. NNW Barro de Navidad. COLIMA: Colima (Hall and Kelson, 1959); Manzanillo (Merriam, 1892); *Juárez* (Laurie, 1953); Armería (Hall and Kelson, 1959).

Neotoma alleni elattura.—JALISCO: 8 mi. E Jilotlán de los Dolores (Genoways and Jones, 1972). MICHOACAN (Kelson, 1952): La Huacana; 7 mi. S Tumbiscatio. MORELOS: Cañon del Lobo, 6 mi. W Yautepec (Davis and Russell, 1954); Puente de Ixtla (Kelson, 1952). GUERRERO: Cuapongo, near Chilpancingo (Osgood, 1938; Kelson, 1952).

Neotoma alleni guerrerensis.—GUERRERO: El Limón (Hall and Kelson, 1959); 5 mi. SE Tecpan (Hall and Kelson, 1959); Acapulco (Goldman, 1938).

Neotoma alleni vetula.—PUEBLA: Tehuacán (Merriam, 1894). OAXACA: Teotitlán (Hooper, 1947; Goodwin, 1969). GUERRERO: Tlalixtaquilla (Hall and Kelson, 1959).

FOSSIL RECORD. Hibbard (1967) suggested that the evolutionary lineage that eventually gave rise to *Neotoma* must have diverged from a generalized cricetine in the Upper Miocene; he considered the extinct genus *Pliotomodon*, named from mid-Pliocene deposits in California (Hoffmeister, 1945), a side branch related to the *Neotoma* lineage rather than a direct ancestor of Recent woodrats. *Parahodomys spelaeus*, a distinctly woodrat-like fossil, was described from the mid-Pleistocene Cumberland Cave of Maryland by Gidley and Gazin (1933). This genus, as described in a later report by these authors (1938), had cheekteeth that were "in general structure as in *Hodomys*, but with re-entrant valleys, especially the external ones, shallower and directed nearly at right angles to the toothrow. [They are directed more obliquely forward in *Hodomys*.]" The last lower molar (m3) of *Parahodomys* possessed a posterointernal re-entrant valley that was lacking in *Hodomys*. Hibbard (1941*a*) described *Parahodomys quadriplicatus* from the Rexroad Fauna of the late Pliocene of southwestern Kansas. He later noted (1941*b*) that the lower dentition of *P. quadriplicatus* differed as much from *P. spelaeus* as *P. spelaeus* did from *N. alleni*. He believed that *Parahodomys* was not ancestral to any of the modern subgenera of *Neotoma*, but of them it probably was most closely related to the *Teanopus* line.

In 1967, Hibbard described the subgenus *Paraneotoma* of the genus *Neotoma*, including in it as the type species *Parahodomys quadriplicatus* (Hibbard, 1941*a*). He pointed out that the m3 of *Parahodomys spelaeus* would not wear to the S-shaped pattern typical of *Neotoma alleni*, but that the m3 of *Neotoma* (*Paraneotoma*) *quadriplicatus* would wear to give this pattern. In addition, he described two new species of this subgenus—*Neotoma* (*Paraneotoma*) *sawrockensis* and *Neotoma* (*Paraneotoma*) *taylori*. The former was from the lower late Pliocene Saw Rock Canyon local fauna and the latter was the middle Pleistocene Borchers local fauna (see Hibbard, 1970). Hibbard (1967) stated: "It is not possible at the present time to demonstrate from tooth characters that *N.* (*Paraneotoma*) *quadriplicatus* is ancestral to the later groups of Recent *Neotoma*. It appears that it is closely related to or is the stock that gave rise to *N. alleni*."

Alvarez (1966) described *Neotoma magnodonta* from a late Pleistocene deposit near Tequesquinahua, México. Alvarez believed that assignment of this species to the subgenus *Hodomys* was probably correct, but could not be made definite based upon the available material. If it is assignable to the subgenus *Hodomys*, *N. magnodonta* is an advanced species and probably is not ancestral to *Neotoma alleni*.

FORM. The baculum of *Neotoma alleni* was described by Burt and Barkalow (1942) and Burt (1960). This structure has a broad base that is deeply concave ventrally and slightly concave dorsally. This section of the baculum resembles that of *N. floridana* except that it is not as deep and the concavity is less pronounced. The round shaft is slightly curved dorsally at the distal end and terminates in a small knob. In this feature it resembles *N. albigula*. Measurements (in millimeters) of two specimens from Jalisco given by Burt (1960:61) are length of the baculum, 6.0, 6.8, and width of the base of the baculum, 2.4, 3.0.

The glans penis of *Neotoma alleni*, which was described by Hooper (1960), resembles this structure in *Xenomys* in several important traits. The glans is approximately twice as long as its greatest width and is about one-fourth the hind foot length. The surface of the glans is indented by shallow mid-dorsal and mid-ventral troughs, the latter bearing a raphe. The epidermis is covered with spines, each minute, sharp, and recessed within a pit. The spineless, shallow terminal crater is nearly filled with a bulbous mass of soft tissue covering the cartilaginous cap of the baculum. This mass is entirely free of the crater walls. A small, conical, soft papilla is present middorsally at the base of the bulbous mass. The urethra terminates in the crater with the mid-ventral lip of its meatus prolonged distally as a pair of thick, obtuse, urethral processes.

The hyoid apparatus of *Neotoma alleni* was described and figured by Sprague (1941:309). He found that *N. alleni* resembled *Xenomys nelsoni* in this structure. Measurements (in millimeters) for one specimen were as follows: width of basihyal, 6.7; length of thyrohyal, 4.9; length of ceratohyal, 2.1; arch of the basihyal and thyrohyals, 6.0; width of the thyrohyals, 10.1; thickness of the basihyal through the entoglossal process, 2.4.

Carleton (1973) studied the gross stomach morphology of *N. alleni* and compared it to members of all subgenera of *Neotoma* and to some other cricetine genera. He classified the stomach of *alleni* as being of a bilocular-intermediate type, with the intermediacy apparently referring to a position between the hemiglandular and discoglandular stomachs of certain other groups. Carleton reported: "The bordering fold in [*alleni*] crosses the lesser curvature at a point midway to the incisura angularis and pyloric orifice, and then angles deeply into the antrum. Recurving tightly, the fold returns to intersect the greater curvature opposite the opening of the esophagus." The *incisura angularis* and *fornix ventricularis* were found to resemble closely those structures of other woodrats. However, the distribution of glandular epithelium in *alleni* was found to be more extensive than in other *Neotoma*. In this respect, Carleton considered the stomach of *alleni* more like that of certain species of *Reithrodontomys* than like other species of *Neotoma*.

No other data are available certaining the post-cranial skeletal or soft anatomy of *Neotoma alleni*.

ECOLOGY. Merriam (1892, quoting from E. W. Nelson's field notes) stated that *N. alleni* in the vicinity of Manzanillo, Colima, was everywhere on the lower wooded slopes and the adjacent dry ground that was covered with mesquite. Nelson noted the burrows of *N. alleni* at the base of trees and under other available cover. Numerous trails were noted leading from these burrows onto the wooded hillside. In a few places, but

rarely, Nelson noted small collections of sticks, shells of land crabs, and other *Neotoma* bric-a-brac, especially where the rats were living in ledges of loose rock.

Near Tehuacán, Puebla, Nelson (Merriam, 1894) found *N. alleni* to be rather common about the foot of low cliffs and rocky ledges on the hillsides east of the city, and noted that it inhabited dense patches of agave. Numerous trails led along the hillside from rock to rock or to the cover of agave patches, and between neighboring groups of these plants. No signs of nest building were seen by Nelson in this area.

In southern Sinaloa, Birney and Jones (1972) found this species to be an inhabitant of dense, thorny scrub along the Río de la Cañas and on two barrier islands. Along the Río de la Cañas, rats were found to occupy flood debris that had accumulated under the brush. Nests on the barrier islands were found in debris and at bases of trees, and some rats occupied holes under logs and around tree roots. On Isla Palmito de la Virgen, P. L. Clifton heard several Allen's woodrats calling shortly after dark; he likened the call to that of *Ochotona princeps*, whereas Schaldach (1960) heard calls that were emitted in a long series of clear staccato "chooks."

In Jalisco, Genoways and Jones (1973) reported that this species was taken in a variety of situations including a rock fence, the base of a rock cliff, dense tropical deciduous forest along a stream, and a small cave in an area of tropical vegetation. Davis and Russell (1954) also reported a specimen taken in a cave in Morelos. At 5 km. NNW of Barro de Navidad, Jalisco, M. R. Lee (Genoways and Jones, 1973) obtained specimens of this species in the boulders at the base of a cliff. A grove of coco-oil palms was situated near the base of the cliff. Lee noted that *N. alleni* did not construct large nests of sticks and debris characteristic of other woodrats, the only evidence of its presence among the boulders being droppings and caches of coco-oil nuts. Other species of rodents taken along with *N. alleni* in Jalisco were *Spermophilus adocetus*, *S. annulatus*, *Sciurus aureogaster*, *Liomys pictus*, *Pappogeomys tylorhinus*, *Orthogeomys grandis*, *Peromyscus banderanus*, *P. boylii*, *P. maniculatus*, and *Neotoma mexicana*.

Emerson (1971) reported the anopluran louse, *Neohaematopinus neotomae*, from *N. alleni* in southern Sinaloa.

REPRODUCTION AND DEVELOPMENT. One specimen (KU 64549) in the Museum of Natural History, The University of Kansas, from near Valle de Banderas, Nayarit, was noted as containing a single embryo that measured 16 mm in crown-rump length on 3 February 1955. Birney and Jones (1972) reported a lactating female accompanied by two young when chased from a house in Sinaloa on 3 September 1962. They report juveniles, approximately a month old, taken along the Río de la Cañas on 17 February 1961 and 15 August 1969. Another juvenile was taken 10 mi SE Tuxpan, Jalisco, on 5 September 1966 (Genoways and Jones, 1973). Two males trapped in late February in Sinaloa each had testes that measured 16 mm.

Genoways and Jones (1973) described three maturational pelages in material from Jalisco. Juvenile pelage was dark slate to blackish, with only a few reddish-brown hairs visible dorsally. Subadult pelage was described as being pale grayish in color containing numerous reddish-brown hairs dorsally, thinning on sides. Pelage of adults is characterized by reddish-brown or tawny-red color both dorsally and laterally.

GENETICS. The karotype of a female from 27 km S of Escuinapa, Sinaloa, is the only one known for the species (figure 4). This individual possessed 48 chromosomes of which one pair was large-sized subtelocentrics, one pair was medium-sized submetacentrics, and the remaining 22 pairs formed a graded series of telocentrics. Some chromosomes judged to be telocentric probably possess a minute second arm. At present, the sex chromosomes of this species are unknown because only a female has been karyotyped; however, based upon data from other species of *Neotoma*, the large pair of subtelocentrics may represent the sex chromosomes. The karyotype of *Neotoma alleni* is unique among woodrats thus far karyotyped. Baker and Mascarello (1969) found that members of the subgenus *Neotoma* had 52 (six species) and 56 (one species) chromosomes, the sole member of the subgenus *Teonoma* had 54 chromosomes, and the only member of the subgenus *Teanopus* had 38 chromosomes.

REMARKS. Although *Neotoma alleni* occupies a rather extensive geographic distribution in western and central México, it is evidently only locally abundant. Much remains

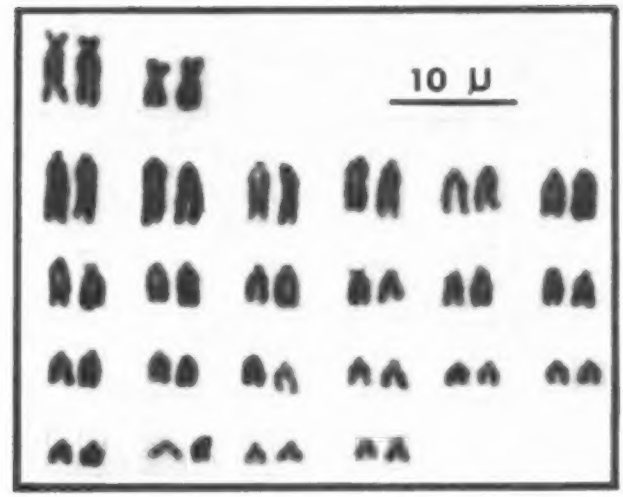

FIGURE 4. Karyotype of a female *Neotoma alleni alleni* from 27 km S Escuinapa, Sinaloa, (TTU 8410). Karyotypic material and figure supplied by Robert J. Baker.

to be learned about the biology of this unique species. We have been unable, for instance, to locate any data in the literature on the physiology of *alleni*. Ecologically the species is evidently most abundant in areas of thorny scrub or agave. Goldman and Moore (1946) listed *Neotoma alleni* as one of the characteristic species of their Nayarit-Guerrero Biotic Province, although it occurs in at least two other of their provinces. Goldman (1951) listed *N. alleni* with species from the Lower Tropical and Lower Austral life zones of México.

Merriam (1892) originally described this species as a member of the genus *Neotoma*. However, 2 years later (Merriam, 1894), he described the genus *Hodomys* with *Neotoma alleni* as the type species. Also in this publication, he named another species, *Hodomys vetulus*, to be included in this genus. The genus was considered to be distinct until Burt and Barkalow (1942) examined bacula and crania of woodrats and concluded that *Hodomys* should be reduced to subgeneric rank within the genus *Neotoma*. Subsequently, generic status for *Hodomys* has been recommended by Schaldach (1960) following a study of the habits of *N. alleni* and *Xenomys nelsoni*. Carleton (1973) supported this recommendation after comparative study of gastric morphology of cricetine rodents, including 12 species of woodrats (with *alleni*). We have considered this arrangement seriously and believe it has merit. However, we elected to continue to recognize *Hodomys* as a subgenus of *Neotoma* until more is known of the affinities of *Xenomys nelsoni*. Additional information may indicate that a more reflective classification would include *Xenomys* within *Neotoma* rather than to recognize both *Hodomys* and *Xenomys* as monotypic genera. Kelson (1952) examined the status of the two nominal species of *Hodomys* and concluded that they represented a single species with four recognizable subspecies.

The authors choose to treat the Cricetidae as a full family rather than as a subfamily of the Muridae, as done in other accounts of mammalian species.

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